

THE NUTRITION OF *PARANEMERTES PEREGRINA*
(RHYNCHOCOELA: HOPLONEMERTEA). I. STUDIES
ON FOOD AND FEEDING BEHAVIOR¹

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Nemerteans are common organisms in the intertidal zones of temperate regions of the world (Coe, 1943). They live in a wide variety of habitats and can occur in large numbers. Most nemerteans are carnivorous (Coe, 1943), and as abundant predators they may well be important components of the communities in which they live. Since efficient exploitation of available food is a necessary requirement of all animals, studies of feeding and food preference should be of great importance to the field of ecology (Emlen, 1966). Both because of their predatory nature and because they have an interesting means of capturing food, nemerteans are well suited to the study of feeding and food preference.

This paper reports aspects of feeding behavior of *Paranemertes peregrina* Coe, 1901, hereafter referred to as *Paranemertes*, a predatory nemertean which occurs along the entire Pacific coast of North America from the Aleutian Islands in Alaska to Ensenada, Mexico (Coe, 1940) in both rocky and muddy bay intertidal habitats. The feeding habits of *Paranemertes* have previously received little attention, being only briefly mentioned by Coe (1905), MacGinitie and MacGinitie (1949), and Correa (1964). The MacGinities (1949, and personal communication) reported that *Paranemertes* feeds at low tides on nereid polychaetes.

Specifically, this report concerns (1) a description of the feeding process of *Paranemertes*, including steps in prey capture; (2) a comparison of *Paranemertes* from exposed and sheltered rocky intertidal and muddy bay areas for food in nature and food preferences in laboratory experiments; and (3) a description of an escape response of nereid prey to *Paranemertes*. This study is the beginning of an ecological study now in progress on the role of *Paranemertes* as a predator in these types of communities.

MATERIALS AND METHODS

Four study areas were selected where *Paranemertes* is fairly abundant. These were: (1) English Camp at Garrison Bay, San Juan Island, Washington, a protected muddy bay area; (2) the ferry landing at Edmonds, Washington, a concrete and metal structure with large boulders piled against it; (3) boulders on the sandy beach to the north of the ferry landing at Edmonds; and (4) the rocky outcropping at Mukkaw Bay, south of Cape Flattery, open Pacific coast,

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Washington. Garrison Bay and the two rocky areas at Edmonds are in protected waters; Mukkaw Bay is exposed to strong wave action. *Paranemertes* was found on the mud at Garrison Bay, and among and below the barnacles and mussels on the rocks in the other areas.

Field observations and collections of over 500 *Paranemertes* were made at the four study areas during low tides from October 1966 through April 1967, monthly at Garrison and Mukkaw Bays and nearly weekly at Edmonds. Specimens of *Paranemertes* were put singly into 2-oz jars partly filled with clean cooled sea water. All specimens were kept near 10° C.

Polychaetes from each study area were collected to determine what species lived in association with *Paranemertes* and to be used in food preference experiments. Polychaetes were identified from Hartman, 1968 and Berkeley and Berkeley 1948, 1952. Potential prey from other phyla which occurred in these habitats were not used for food preference experiments since initial examinations of *Paranemertes* faeces and initial preference experiments gave positive results only for polychaetes.

Since each nemertean was kept in a separate container, its faeces from food eaten in nature could be collected from the water in which it was kept. *Paranemertes* faeces consist of bundles of polychaete setae, facilitating identification of the prey. Faeces and worms that had fed in nature were preserved in 70% alcohol.

In food preference experiments a potential prey was put into a container with a nemertean which had been kept without food for one week, and the reactions of the nemertean and prey were observed. Reactions of the nemerteans were graded in three categories, after contact was made with the prey. Step 1, absence of reaction or jerking back of the head was considered a negative response. Step 2, eversion of the proboscis, and Step 3, ingestion of prey, were considered positive responses. If a negative response occurred following presentation of a polychaete other than a nereid, a nereid was offered subsequently, since preliminary work indicated that *Paranemertes* has a strong preference for nereids. The experiment was excluded from analysis of results if there was a negative response to the nereid control. Preliminary data suggested that *Paranemertes* has a slight "memory," i.e., a nemertean offered a nereid followed soon by a different food responds positively at first to the second food. This "memory" apparently does not last more than a few minutes. Therefore, if a given *Paranemertes* was used for more than one feeding experiment, it was returned to its container after each experiment and not used again for at least one hour. When possible, each prey type was presented in ten trials. The length of time before defecation was recorded in several instances. Fisher's exact test (Siegel, 1956) was used except where otherwise indicated to examine the significance of food preference results.

An escape response of nereid prey to *Paranemertes* was observed in nature and in *Paranemertes* food preference tests. Experiments were run to determine (1) if nereids responded more vigorously to *Paranemertes* than to simple tactile stimulus and (2) what parts of the nereid body are most sensitive to *Paranemertes*.

OBSERVATIONS AND RESULTS

General observations in nature

Paranemertes is an active predator during low tide. Worms were observed to emerge from crevices and from the mud as the tide receded and they were observed feeding out of water at low tide. They are not merely stranded on the rocks as the tide goes out.

Few *Paranemertes* come out when it is raining, even during low tides. During inclement weather aggregations of *Paranemertes* can be found in cracks or sheltered crevices in rocky areas. *Paranemertes* crawls out into the open more often at night or on cloudy days than it does on sunny days.

Feeding process

Feeding of *Paranemertes* has been analyzed as a 3-step process. Step 1, prey contact: Contact of the anterior edge of *Paranemertes*' head with a prey organism and recoil of *Paranemertes*' anterior end is the first step of the feeding process. This recoil almost always occurs, even if the prey proves an unacceptable species. Recoil is often accompanied by a 90° or a 180° turn of the head away from the prey and a crawling away if the prey is not acceptable. The initial head withdrawal is more vigorous if the prey is a nereid.

Preliminary tests and observations suggested that *Paranemertes* has little or no distance chemoreception for use in finding prey. Nereids had to come into contact with the anterior rim of a *Paranemertes*' head before the nemertean responded. Water from jars in which nereids lived caused no response when pipetted into a jar with a *Paranemertes*. In two of eleven tries, *Paranemertes* responded by slight eversion of the proboscis to the tube of a recently-removed nereid. Once a *Paranemertes* followed the fresh mucus trail of a nereid. Contact with nereids or their immediate and fresh products appears to be a requirement for recognition and elicitation of the feeding response by *Paranemertes*.

Step 2, prey capture: The second step in the feeding process is eversion of the proboscis, often rapidly and with great force. Prey much stronger than the nemertean may be paralyzed within a few seconds by this action. In the laboratory, eversion of the proboscis occurs almost every time a nereid is presented, but only rarely in response to other prey organisms (Tables I-IV). For this reason Step 2 is considered a positive feeding response. In the laboratory *Paranemertes* often paralyzes a nereid, then does not eat it.

The proboscis everts to a given point, stops, then moves again, either inverting or everting more, then stops again. These stops are sometimes accompanied by a visible jabbing motion. The stylet of *Paranemertes* is small (Coe, 1905) and difficult to follow during rapid proboscis movements. However, it was observed moving forward to the point where the end was in contact with the prey. It is believed that the stylet venom is pumped in the prey during these stops. Paralysis is complete only in the part of the prey around which the proboscis has been wound, and often a nemertean must envelop the prey 3 or 4 times in different places before the effect is complete. The proboscis can be everted a short or long distance and the stylet can be terminal in either case. When the nemertean is through puncturing the prey in one place, it can with-

draw the stylet, evert the end of the proboscis still more, and stab in a new and more distant place on the prey. The initial force for eversion is hydrostatic (Bohmig, cited by Clark, 1964), but further, more deliberate eversion appears to be controlled by the proboscis musculature. Either the central stylet is replaced with great rapidity or *Paranemertes* does not lose its stylet readily. Proboscides cut off while wrapped around a prey or shortly thereafter always showed the central stylet intact and always showed accessory stylets in the accessory sacs. The proboscis often winds tightly around the prey, and combined effects of prey movement, squeezing, and stylet action frequently cause the prey to tear apart. However, if the prey is not badly damaged, or if it is fairly large, the effect of the venom wears off in about 20 minutes. The venom paralyzes but does not kill the prey.

The proboscis is lined with conical gland cells that secrete a sticky mucus-like substance upon contact with a prey, enveloping the prey where the proboscis was wrapped around it. This sticky substance functions to hold the prey and may have some paralytic function as well.

Step 3, ingestion: After a prey is paralyzed *Paranemertes* withdraws the proboscis, losing contact with the prey for a few seconds. It then moves over the prey, feeling for a place to start the sucking-ingestion process, the third of the feeding stages. *Paranemertes* will start sucking any place on the prey which it can surround with its distended mouth. Prey can be ingested tail or head first, or be bent into a v- or j-shape and ingested from the side. Muscular peristalses from the posterior tip anteriorad often accompany ingestion. Most of ingestion is accomplished by the musculature around the mouth. There are sometimes posterior-to-anterior peristaltic waves of the region just posterior to the mouth. The lips also expand lengthwise, then close over a new portion of the prey, then contract, drawing in the prey. Sometimes small prey seem to be glided in as if by ciliary action. If a prey begins to move during ingestion, or if the prey is large and the *Paranemertes* is having difficulty ingesting it, the proboscis is often everted even while the anterior end is highly distended. When prey diameter is less than the distended mouth, ingestion only takes a few minutes; the entire feeding process can take place in 2 to 3 minutes. The limiting factor in ingestion is prey diameter. *Paranemertes* cannot ingest a prey whose diameter is far greater than its own. Prey length makes little difference. One *Paranemertes* was observed eating a nereid longer than itself.

Slight variations in the feeding process occur when syllids or spionids are eaten. The greatest differences were observed during feeding on *Syllis*. Even though the syllid hardly moved, the nemertean everted its proboscis more than 10 times, yet the syllid was hardly affected, suggesting that syllids might be partially refractory to the venom. A posterior piece of the syllid was broken off, and the proboscis continued to entwine the piece. Ingestion took several minutes even though the syllid was thin and only about an inch long, and the piece being ingested even smaller. Eating consisted of tearing a piece off, wrapping the proboscis around that piece, ingestion, then repeating the process on another piece further anterior.

On a few occasions, when a *Paranemertes* was offered a nereid that had been previously paralyzed, step two was skipped.

Length of time before defecation

Observations of 12 specimens of *Paranemertes* every 2 hours after laboratory feedings showed that defecation occurs from 12 to more than 33 hours after feeding. Observations at longer intervals from field collections and laboratory feedings gave the same results.

Observations of feedings in nature

At Garrison Bay 44 of 246 specimens of *Paranemertes* collected (18%) were observed feeding or defecated shortly after being taken to the laboratory. Of those that had fed in nature, 36 (81.8%) had eaten *Platynereis bicanaliculata*, 7 (15.9%) had eaten other nereids (setae of nereids other than *Platynereis* were not identifiable to species), and only 1 (2.3%) had fed on a non-nereid polychaete. A total of 97.7% had eaten nereid prey.

At Mukkaw Bay 8 of 42 worms collected (19%) had recently fed, all on nereid prey, and probably all on *Nereis vexillosa* as that was the only nereid species found in that habitat.

Twenty of 56 worms (35%) collected at Edmonds beach had recently eaten. Seven of these were observed feeding. Food at this habitat consisted of 11 nereids (probably *N. vexillosa*) (55%), 8 *Polydora* sp. (40%), and 1 *Syllis* sp. (5%). Although the majority of worms from Edmonds beach had fed in nature on nereids, the nemerteans from this location had a more varied diet than did those at Garrison or Mukkaw Bays.

At the Edmonds ferry landing 33 of 140 worms collected (23.5%) had recently fed. Six of these were observed while feeding. The diet at the ferry landing consisted of 22 (67.7%) *Syllis* sp., 8 (24.2%) *Polydora* sp. and 3 (9.1%) *Lepidonotus squamata*. No nereid faeces were collected from *Paranemertes* from the ferry landing. Nereids were quite rare in numerous polychaete samples from the ferry landing rocks, and were probably too scarce to constitute much of the diet of *Paranemertes*.

Food preference experiments

Tables I-IV show possible prey species tested with *Paranemertes* from each study area. In most cases prey species found in a given study area were tested with *Paranemertes* from the same area. However, *Platynereis* was tested with *Paranemertes* from all study areas even though it was found only at Garrison Bay. Members of all macroscopic polychaete families collected from each area were tested. One *Neanthes brandti* (Nereidae) was found at Garrison Bay, and individuals of *Paranemertes* have been observed attacking *Neanthes*. However, adults are far too large for the nemerteans to be able to ingest; they were therefore not considered in laboratory experiments.

In the tables, steps 1, 2 and 3 refer to feeding reactions of *Paranemertes* to the prey. Step 1 is considered a negative response, steps 2 and 3 are considered positive responses. The column "total positive trials" sums all trials in which a *Paranemertes* responded positively either to a test prey or to a control nereid. The column "negative responses to controls" refers to the number of trials in

TABLE I
Feeding experiments with Garrison Bay *Paranemertes*

Food	Steps in feeding response			Total positive trials	Negative responses to nereid controls
	Initial Step 1	Final			
		Step 2	Step 3		
<i>Lumbrineris inflata</i>	5			5	4
<i>Ophiodromus pugettensis</i>	10			10	0
<i>Nainereis laevigata</i>	11			11	2
<i>Glycinde</i> sp.	6			6	3
<i>Dorvillea</i> sp.	8			8	1
Cirratulid	8	1		9	1
Terebellid	5			5	5
Phyllodocid	8			8	2
<i>Polydora</i> sp.	7	1		8	2
<i>Lepidonotus squamatus</i>	6		1	7	0
<i>Armandia brevis</i>	9		1	10	1
<i>Nereis vexillosa</i>	1	5	5	11	—
<i>Platynereis bicanaliculata</i>	10*		17	27	—
	—	—	—	—	—
Totals	94	7	24	125	21

* These worms were fed by invertebrate zoology students. I do not know if the worms responded at Step 1 or Step 2. These data are conservatively listed as negative responses.

which a *Paranemertes* did not respond to either test or control prey. There were no controls when nereids were the test prey.

In the laboratory specimens of *Paranemertes* from Garrison Bay show a very strong preference for nereids (Table I). In only one case was any other polychaete ingested, and in only 4 of 87 tries did a *Paranemertes* react positively to other possible prey organisms. The nemerteans from Garrison Bay did not prefer one nereid species to the other (χ^2 test with Yates' correction: $P > 0.5$).

Although there are few experiments with specimens of *Paranemertes* from Mukkaw Bay, results show (Table II) a significant difference in response by

TABLE II
Feeding experiments with Mukkaw Bay *Paranemertes*

Food	Steps in feeding response			Total number of trials
	Initial Step 1	Final		
		Step 2	Step 3	
Phyllodocid	5			5
<i>Syllis</i> sp.	8			8
<i>Nereis vexillosa</i>		10	1	11
<i>Platynereis bicanaliculata</i>	1	10	1	12
	—	—	—	—
Totals	14	20	2	36

TABLE III
Feeding experiments with Edmonds Beach Parameletes

Food	Steps in feeding response			Total positive trials	Negative responses to controls
	Initial Step 1	Final			
		Step 2	Step 3		
<i>Hemipodus borealis</i>	7			7	0
<i>Polydora</i> sp.	9			9	2
<i>Syllis</i> sp.	8	1		9	2
<i>Eteone</i> sp.	10			10	2
<i>Lepidonotus squamatus</i>	7	1		8	1
<i>Nereis vexillosa</i>	1	5	1	7	—
<i>Platynereis bicanaliculata</i>	2	3	4	9	—
	—	—	—	—	—
Totals	44	10	5	59	7

Pairs with Significant Difference at the 5% Level (Fisher's Exact Test)

<i>Nereis</i> — <i>Syllis</i>	$P = 0.01$
<i>Nereis</i> — <i>Polydora</i>	$P < 0.005$
<i>Nereis</i> — <i>Lepidonotus</i>	$0.025 > P > 0.01$
<i>Nereis</i> — <i>Eteone</i>	$P < 0.005$
<i>Nereis</i> — <i>Hemipodus</i>	$0.01 > P > 0.005$
<i>Platynereis</i> — <i>Lepidonotus</i>	$P = 0.025$
<i>Platynereis</i> — <i>Polydora</i>	$P = 0.005$

TABLE IV
Feeding experiments with Parameletes from Edmonds Landing

Food	Steps in feeding response			Total positive trials	Negative responses to controls
	Initial Step 1	Final			
		Step 2	Step 3		
<i>Syllis</i> sp.	9	4	2	15	2
<i>Polydora</i> sp.	7	3	3	13	0
<i>Lepidonotus squamatus</i>	10	1		11	1
<i>Hemipodus borealis</i>	8	1		9	0
<i>Eteone</i> sp.	8			8	0
<i>Nereis vexillosa</i>		6	4	10	—
<i>Platynereis bicanaliculata</i>		3	5	8	—
	—	—	—	—	—
Totals	42	18	14	74	3

Pairs with Significant Difference at the 5% Level (Fisher's Exact Test)

<i>Platynereis</i> — <i>Syllis</i>	$0.025 > P > 0.01$
<i>Platynereis</i> — <i>Polydora</i>	$0.05 > P > 0.025$
<i>Platynereis</i> — <i>Lepidonotus</i>	$P < 0.005$
<i>Platynereis</i> — <i>Hemipodus</i>	$P < 0.005$
<i>Platynereis</i> — <i>Eteone</i>	$P < 0.005$
<i>Syllis</i> — <i>Eteone</i>	$P = 0.05$
<i>Polydora</i> — <i>Eteone</i>	$P = 0.05$

Paranemertes to *Nereis* or *Platynereis* and syllids ($P < 0.005$) and to *Nereis* ($0.01 > P > 0.005$) or *Platynereis* ($P = 0.005$) and phyllodocids. There was no significant difference in response to the nereid species offered. It can be concluded that Mukkaw Bay individuals also prefer nereid over non-nereid food.

There was a significant difference in the response of specimens of *Paranemertes* from Edmonds beach to *Nereis* or *Platynereis* and to non-nereid foods. There was no significant difference in responses among the non-nereid species, and there was no significant difference in response between the nereid species offered (Table III). It can be concluded that Edmonds beach individuals also prefer nereid over non-nereid food and have no preference among the nereids.

Specimens of *Paranemertes* from Edmonds ferry landing again showed preference of nereids to all other prey, and there was no significant difference in the response to the two nereid species offered. The nemerteans reacted positively to *Syllis* and *Polydora*, and even ingested them, and there was a significant difference at the 5% level in the response of *Paranemertes* to these two species and *Eteone*, to which *Paranemertes* showed total lack of response.

Differences between nereids

Although specimens of *Paranemertes* showed no significant preference of one nereid over another, there was a significantly greater number of successful feedings during the food preference tests when *Platynereis* was the prey than when *Nereis vexillosa* was the prey. Several times *Paranemertes* could not find a place on *Nereis* from which to start the sucking ingestion process (step 3 of the feeding process). If trials in which step 3 was started, but in which *Paranemertes* derived no nourishment from the prey, are combined with step 2 as unsuccessful positive trials (Table V), *Paranemertes* was significantly more successful in feeding on *Platynereis* than on *Nereis vexillosa* ($\chi^2 = 5.957, 0.02 > P > 0.01$).

Nereis vexillosa appears to be a more aggressive animal than *Platynereis*. On several occasions during feeding experiments a *Nereis* bit a *Paranemertes*' proboscis when the proboscis was wrapping around it. The *Nereis* sometimes

TABLE V
*Unsuccessful positive responses versus completed feedings by
Paranemertes to Platynereis and Nereis*

Source of experimental animals	Food	Unsuccessful positive responses	Complete feedings
Garrison Bay	<i>Nereis vexillosa</i>	6	4
	<i>Platynereis bicanaliculata</i>	10	17
Mukkaw Bay	<i>Nereis vexillosa</i>	10	1
	<i>Platynereis bicanaliculata</i>	11	0
Edmonds Beach	<i>Nereis vexillosa</i>	5	1
	<i>Platynereis bicanaliculata</i>	4	3
Edmonds Landing	<i>Nereis vexillosa</i>	9	1
	<i>Platynereis bicanaliculata</i>	4	4
Totals	<i>Nereis vexillosa</i>	30	7
	<i>Platynereis bicanaliculata</i>	29	24

did not let go for more than an hour, making the feeding process very drawn out. On one occasion a *Nereis* bit the tail off a *Paranemertes*. These actions were never observed when *Platynereis* was the prey. Small *Nereis* were used for feeding experiments; however, *Nereis* as small as some *Platynereis* used were difficult to find. Size difference might account for part of the increased difficulty *Paranemertes* had with *Nereis*.

Nereid escape response

It was observed, both in nature and in the laboratory food preference tests for *Paranemertes*, that nereid polychaetes have an escape response from *Paranemertes*. Nereids swim rapidly away upon contact with *Paranemertes* if water is present. If they cannot swim, as is often the case during low tides in nature when *Paranemertes* is feeding, they jerk away and crawl off rapidly. Responses of nereids in tests to determine if nereids responded to *Paranemertes* more strongly than to simple tactile stimulus and to determine their more sensitive parts were categorized as five levels (Table VI). Data from *Nereis v. villosa* and *Platynereis* were similar

TABLE VI
Responses of nereids to Paranemertes and to tactile stimulus

Part of nereid touched	Response to <i>Paranemertes</i>				
	Degree of response				
	0	1	2	3	4
	Number of times response reached				
Palps or anterior end	2	0	4	0	1
Parapodia	0	0	1	0	2
Dorsum or venter	0	0	1	0	4
Posterior cirri	0	0	6	3	5
	Response to tactile stimulus				
Posterior cirri	4	2	1	0	0

Degree of response by nereids to *Paranemertes* or to tactile stimulus

0 = neutral

1 = slight increase in crawling rate

2 = jerk and rapid crawling

3 = flip of tail and rapid crawling

4 = swimming

and are lumped. Response to tactile stimulus was determined only for a sensitive part of the nereids, the posterior cirri.

If response levels 0 and 1 are considered negative and levels 2, 3, and 4 are considered positive responses, there is a significant difference ($\chi^2 = 15.90$, $P < 0.001$) between nereid response to *Paranemertes* and to tactile stimulus from a pencil or probe. Fisher's exact test shows no significant difference in response

from any one of the four body parts tested. The difference between response to tactile stimulus and response to *Paranemertes* of nereid palps was not significant at the 5% level, but the difference was significant for the other three areas tested (parapodia—tactile stimulus, $P = 0.05$; dorsum—tactile stimulus, $0.025 > P > 0.01$; posterior cirri—tactile stimulus, $P < 0.005$).

Although very few trials were made, nereids did not respond with the swimming escape response when they came into contact with *Amphiporus formidabilis*, *Emplectonema gracile*, or *Zygonemertes virescens*, other nemerteans which occur in the same habitats with *Paranemertes* and the nereids, but which to my knowledge, do not eat nereids.

DISCUSSION

The feeding process of *Paranemertes* differs in only minor details from feeding reported for other vermivorous nemerteans. For example, heteronemerteans as *Lineus* do not lose proboscis contact with the prey while searching for a place to start ingestion (Beklemishev, 1955; Jennings, 1960); *Paranemertes* can afford such behavior since it paralyzes its prey. *Paranemertes*, like *Cephalothrix* species (Jennings and Gibson, 1969), cannot ingest polychaetes that are much greater in diameter than it is. *Lineus* can ingest prey several times its diameter (Gontcharoff, 1948; Beklemishev, 1955). *Paranemertes* has no distance chemoreception for finding food; *Prostoma* (Reisinger, 1926), *Cerebratulus* (Wilson, 1900; Coe, 1943), and two species of *Lineus* (Jennings and Gibson, 1969) all find prey by long range chemoreception.

A major difference between feeding of *Paranemertes* and most other nemerteans is the high degree of specificity in food preference in *Paranemertes*. *Amphiporus lactifloreus* was reported to have narrow preference for *Gammarus locusta* in laboratory feedings (Jennings and Gibson, 1969), but most nemerteans studied so far eat a wide variety of prey (Roe, 1967; Gibson, 1968, 1970). The specialized preference of *Paranemertes* for nereids in the laboratory is reflected in nature by the high percentage of nereid food in the diet in areas where this preferred food is available. Although *Paranemertes* at the Edmonds ferry landing did not eat nereids because they were unavailable, these same nemerteans showed strong preference for nereid food in the laboratory experiments. These *Paranemertes* are quite small, even as mature adults, compared to the sizes of Garrison and Mukkaw Bay *Paranemertes*. Their small size is possibly an effect of the lack of preferred food in their diet. *Paranemertes* may be able to capture nereids with much less energy expended per unit energy gained than they can with other prey, as evidenced by the difficulty of feeding by *Paranemertes* on syllids. *Paranemertes* seems to have an optimal feeding strategy by specializing on nereids when they are available and taking a wider range of prey when nereids are uncommon. A maximum of selectivity in food types when food is common, and a decrease in selectivity when food is scarce is the optimal feeding strategy for predators (Emlen, 1966).

The absence of distance chemoreception in *Paranemertes*, combined with its highly specialized predation behavior and diet, plus the well-developed escape response of nereids to it suggest a pattern of evolution in environments where preferred food is so common that distance chemoreception is unnecessary.

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SUMMARY

1. *Paranemertes peregrina*, an abundant hoplonemertean in rocky and muddy intertidal habitats of Washington, feeds on polychaetes during low tide periods.

2. Feeding by *Paranemertes* involves three steps. The first stage is a recoil of the *Paranemertes'* head upon contact with a prey. Contact must be made with the prey; *Paranemertes* does not find prey by distance chemoreception. The proboscis is everted and wraps around the prey in step two. The prey is temporarily paralyzed or is killed. In step three the prey is ingested by means of sucking motions from muscles around the mouth. Defecation occurs from 12 to 33 hours after feeding.

3. Specimens of *Paranemertes* ate mainly nereid polychaetes at the three study areas where nereids were available. At the fourth study area the nemerteans ate a wider variety of polychaetes. Experiments to test food preference showed that specimens of *Paranemertes* from all study areas strongly preferred nereids to members of other polychaete families.

4. Nereid polychaetes have a swimming escape response from *Paranemertes*.

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